# XXVIII.—*The Origin of the Vertebrate Skeleton**.

By Harry G. Seeley, St. John's College, Cambridge.

## § 1. *The Problem of Osteology.*

The facts of comparative osteology are the growth of similar constituent bones of skeletons to different extent and in different directions in the several groups of vertebrate animals. Hence to the palæontologist the discovery of new types of life in the strata usually means a new and limited growth of a few elements of the skeleton in definite directions. These peculiarities of growth give the skeletons which they characterize a plan of structure which differs from that of other animals; and therefore that plan becomes comparable with the plans of growth which distinguish the several known groups. The multitudinous array of species is so reduced to a few factors; and these limiting facts enable the student to investigate and discover the relation of one animal to the remainder, and of all animals to each other, in a manner not dissimilar and with similar success to the way by which meridians of longitude and parallels of latitude localize geographical districts. The biological problem admits of infinite complication, from the skeleton being composed of many different bones, each of which has its definite form, which may vary a little in every species of the group. And though a few general plans may accurately be spoken of as limiting and comprising this vast difference of detail, yet there is no plan except that which is manifested in each and all of the individuals forming the species which the group includes. And if it be necessary, as it is, to see how closely one plan of structure approximates to other plans, or how it differs from them, such a result can only be attained by comparing and contrasting individuals which manifest the kind of growth which is named the plan of the group.

Here comparative osteology offers for investigation the subject of growth of bone. And if a sufficient elucidation of that question can be given, less difficulty will be experienced in understanding the nature of the special growths in specified directions which give a common plan to each of the several zoological groups of Vertebrata named orders.

The skeleton, however, is but a degraded portion of the organism; and, in the kinds of animals which inhabit the world now, the *functions* of the several bones are often known, as well as the nature and modifications of the soft structures, nerves, vessels, viscera, muscles, which are correlated with

* Being an introductory chapter from the Author's MS. 'Osteology of the Reptilia.'

the different types of skeletons. This has in old times made the comparative anatomy of these living animals more a study of the soft vital tissues than of the hard osseous structures, with which alone the fossil types of life can be compared. It has also had a tendency to make the skeleton seem important chiefly as an index to the nervous or respiratory or other organization of the animal to which it pertains. The skeleton, however, has a distinct morphological importance of its own in classification, probably as significant of near affinity as any part of the organism. And in the endeavour to determine the relations of affinity to each other of the fossil groups, and their zoological position, it will be necessary to adhere to this simple morphological test, as well as to apply it to the living ordinal groups, which will hereafter be examined.

The skeleton nevertheless often, in some of its elements, manifests convincing evidence of the condition of some of the soft parts, being subservient to them; and this gives an empirical evidence of affinity which the traditional practice of anatomists would warrant us in valuing highly. Still that estimate of the soft parts of an animal which makes the salient features of all animal classifications will admit of question, and may even seem artificial, when animals are considered in all their affinities. At present, classifications, so far as they are consistent and logical, only express what may be named the lateral affinities of groups of animals—that is, their resemblance to others which are upon the same horizon of organization. But some animal orders also have affinities with other animal orders which are both above and below them in complexity of structures. And if any form of creation by physical and chemical law is admitted into the domain of science, then the affinities which are indicative of evolution must obviously afford a more philosophical ground for classification than those affinities which merely show the parallelism, in their successive stages, of groups of organisms which are parted from each other by inevitable gaps, chasms comparable to those which (as a small illustration) divide from each other the phalanges of the successive digits.

So that we may regard the final problem of comparative osteology as the production, under laws, of a calculus of affinities of animals, in which their relations to each other will be manifest in a classification which transcribes nature herself.

In the following pages a sketch is made of the way in which such a philosophy may be led up to by a consideration of the bones and the fundamental conditions which determine their relations to each other.

## § 2. *The Mechanism of Growth.*

Sir James Paget happily interprets the coexistence of growth of different tissues in the same organism by adopting a doctrine advanced by C. F. Wolff and Treviranus, that each single part of the body, such as fat, muscle, bone, &c., in respect of its nutrition, stands to the whole body in the relation of an excreted substance. Modern chemistry may be considered to have demonstrated that this organized excrement which constitutes the animal, continually excretes itself in other structures, which are capable ot passing naturally out of the body. Even while remaining as constituent in the body, the tissues change from a more live to a less live kind; so that muscle is degraded into urea and fat before the fat is got rid of in carbonic acid and water; and cartilage must first be degraded into bone, the most feebly organic of structures, before it is removed from the body by the natural processes of secretion.

Here, then, the question arises, By the operation of what law are the assimilated parts of our food converted into the tissues which manifest this complemental interrelation of organs? for it would seem probable that there is but one general law governing them all, since, when a bone elongates, almost invariably the muscles, nerves, and vessels which are related to it undergo a corresponding growth.

And the reply to this question will recognize that growth consists of two seemingly different processes:—first, simple increase of substance; and, secondly, differentiation of substance. The increase of bulk is well studied in the individual, while the differentiation of parts can only be observed in the aggregate of individuals which constitute a tribe or order. The tribe-growth has two totally different aspects—in embryology on the one hand, and in morphology on the other; while the chief means for experimental investigation are offered by the mechanical and pathological aspects of growth.

With the comparative anatomist, nerves, muscles, bones, and the other tissues are ultimate facts, as much so as are the different mineral species to the mineralogist; and their essential difference from each other is in chemical composition. They are only to be spoken of, as to origin, as organic colloids separated from each other by continuous organic dialysis. What is named nutrition is no more than dialysis of the nutriment which has been elaborated into blood—a process which is made possible by the disintegrating function of the capillaries of the veins and the repairing function of the arteries. And it comes about by the covering membrane of nerves dialyzing nerve-substance, by the covering of muscular fibres dialyzing muscle-substance, and by the covering of the bones dialyzing osseous substance. Therefore fundamentally the constitution of the body into its anatomical machinery is a matter of chemistry. And on the condition of the blood which supplies the material to be dialyzed, and upon the condition of the dialyzing membranes, depend changes which take place in the chemical composition of organic substances. Thus, under certain conditions, the dialyzing function gets disordered; and then, instead of the body being maintained in healthy equilibrium, pseudomorphs of muscles and bones are produced in other substances, commonly in fat.

Under some circumstances the removal of substances from the body is less rapid than their accumulation; and this produces normal healthy increased growth, which, whether it affect a special muscle or bone or the entire organism, is spoken of as hypertrophy. Under other circumstances the supply of material is less rapid than its removal, and results in a diminution of growth, which is spoken of as atrophy. Now, as the organic degeneration becomes faster or slower, both relatively and actually, than the reconstruction, and *vice versa*, so must all the parts of the body undergo changes in their forms and sizes, which will constitute animals with an infinite variety of shape and stature. But the result of a defective quantity of nutriment is in some cases a smaller tissue, while in other cases the tissue elaborated is of defective quality; and there is as yet no known reason why one of these conditions should prevail rather than the other. If the tissue accumulated is of defective quality, it is probably fat, and in some cases may be bone. On the other hand, the result of superabundant nutriment is in some cases increase and improvement in the quality of the several fibres or particles, and in other cases a multiplication of them; that is, in hypertrophy some parts simply grow large, while in other cases new parts are differentiated. And if hypertrophy and atrophy operate together in the same individual, the result may be that in one organ a new part will be produced, while in another organ an old part will be removed. Thus these natural processes vary not only the shape and aspect of animals, but their structures also.

Hence it follows that the law of nutrition which produces in different individuals of a human family visible difference of form and function, is the same in kind, and only differs in degree from the differentiation which constitutes separate species and genera. In other words, if the hypertrophies and atrophies of individuals could determinate towards special parts, they would inevitably accumulate in the pliable young body when passed onward in successive generations; and there is no inevitable limit to this accumulation or loss of structure, except the maintenance of harmony in the organic functions.

Here, then, the question presents itself, What are the conditions which produce these modifications of the dialyzing action which are manifested in hypertrophy and atrophy? This I now will endeavour to answer. The question may be taken in the abstract. Assuming the amount of nutrient material to remain constant, the change of growth must obviously be due to some change of the conditions which affect the part. Now the only conditions which, while affecting the whole body, may be variable in the different parts, are the forces manifested by the organs in the discharge of their several functions. These act either from within or without; and therefore, as will be generally admitted, every mechanical force acting on the elements of the body is in its effect either of the nature of an impact or of an explosion; and these, with all other forces acting upon and within the animal, can only produce alternations of pressure and tension and rest *. These, therefore, are the stimulants to growth. But growth, being a condition in which the particles expand and increase externally, can only take place when the pressure is removed. And since increase of size can only be resisted by continuous pressure, that, therefore, is the mechanical condition of atrophy. In other words, these mechanical changes are the phenomena which we speak of collectively as exercise. Now the reason why these mechanical actions should produce growth is not far to seek. They alter the conditions of nutrition. Pressure upon a muscle squeezes the blood which was in the veins out of that muscle more rapidly than it usually circulates; and the removal of pressure causes the blood to rush into the part with more force than usual. That is, the establishment in a part of the body of alternate pressure or tension and rest, sets up there a local pump-action which, in effect upon the circulation, is like an additional heart added to that part. It brings more blood to the part, and circulates more food through it; the dialyzing action is carried on faster; and the fibres or cells become plump with abundant food, and new matter is thus fixed in the tissue, and the part has grown.

Therefore since growth, so far as it characterizes the individual and is kinetic, is produced by these mechanical actions, we have to look upon nature and see in what ways the parts of an organism act mechanically upon each other. And should the evidence be conclusive that such actions ac-

* Annals of Nat. Hist. Nov. 1866, No. 107, vol. xviii. p. 347.

tually take place as we have theoretically found should take place, and if they produce the results which theory assigns to them, then the conviction which such phenomena will enforce we may fortify by examples of abnormal growths, due to mechanical causation, afforded by pathology, and test its truth by application to morphology.

In the first place, every organism on the earth's surface has upon it the pressure of the earth's atmosphere—a pressure which, in the case of a man's body, is usually computed at about 70 to 100 tons; and therefore growth can only take place when a force is manifested which is sufficient to lift the atmosphere and hold it up. The skin experiences this pressure, and in consequence, probably, has its superficial epithelial cells flattened to scales. The life is crushed out of them by a pressure which is never appreciably relaxed, and they die under it, and are removed. Such is an example of atrophy. But when the skin is exposed to special extra intermittent pressure, it grows. This relation of growth to pressure was known to John Hunter, and is clearly expounded by him. Generalizing from a consideration of corns, he remarks, in a passage quoted by Sir James Paget:—"The cuticle admits of being thickened from pressure in all parts of the body: hence we find that on the soles of the feet of those who walk much the cuticle becomes very thick; also on the hands of labouring men. We find this wherever there is pressure, as on the elbow, upper part of the little toe, ball of the great toe, &c."

With regard to the internal organs, it would lead me too far away from the object of this writing upon bones to discuss the interrelations of them all. I therefore omit whatever can be dispensed with, and limit myself to what is taught by a few great sets of organs, such as the bones, muscles, nerves, lungs, blood, which show tension and pressure in their functions.

The bones, by supporting each other, act on each other mechanically; for the motion of the body is a succession of falls, which permit alternations of pressure and rest upon the limb-bones. Thus, if we take the humerus, for instance, it will be found most extended in the direction between the radius and the scapula, in which it has, when in mechanical use, to support and lift the weight of the carcass. If the ends are examined, where rotation or movement is permitted, it will be seen that pressure is experienced over a wider area than is possible in the section of the shaft, which only serves as a prop. Hence, and partly from the attachment and pressure of other organs, the articular ends of bones are enlarged; but it is probable that something of the enlarged size of the ends of bones is also due to the vertical pressure causing lateral overgrowth at the joints to be growth in the direction of least resistance, as pointed out by Prof. Humphry.

The bones normally present are dialyzed by the degeneration of the surrounding connective tissue called periosteum, or from the terminal articular or interosseous cartilage. To this periosteum, or to the bone, muscles are for the most part attached, and usually so attached that there is at least one joint between the bones along which they extend. Now the property of a muscle is, that the fibres which constitute it contract and extend. Therefore the very circumstance of their attachment on the bones where there is a condition of yielding implies that when they contract the muscles experience tension; and if the bone does not yield, it experiences pressure or tension from the pull of the muscles. Consequently the attached muscles can undergo no movement without bringing their modifying mechanical influence to bear upon the bones, which is done partly by enabling them to act upon each other, and partly by the intermittent pressure which the periosteum thus is caused to exercise. The same action causes the bones or skin to press against the muscles, and one muscle to press against another. Thus in their exercise the muscles themselves experience this same mechanical condition, which, resulting in a pump-like action, sustains growth.

Of the nerves, only the cerebro-spinal system is sufficiently largely developed to exhibit any visible results of pressure. And here the growth of the brain extends the bones of the brain-case to cover the nervous substance; and when the brain contracts as in old age, the tension of the dura mater upon the bones causes them to thicken, and adapt their inner surface to its reduced size. Similarly the growth of the spinal cord forms the perforation between the neural arch of the vertebra and its centrum; and the perforation enlarges by growth of the vertebral elements with the increase in size of the spinal cord.

The lungs, too, by inspiration and expiration, exert a continuous intermittent pressure upon the ribs; and it may be observed that the ribs are stretched and lifted up at each inspiration. For a considerable period of life this is done with increasing vigour; and during that time the articular cartilages grow. But just as hair, when it has passed through its cycle of growth, grows no more, and dies, and as the particles of the muscles and nerves and other organs which have by exercise undergone the molecular change which has rendered them effete die, and go through new conditions, so a time comes in the life of cartilage when, in normal health, it can no longer form new cartilage-cells; and then there is no further growth of the bone, and the articular cartilage itself gradually becomes thinner. The action of the lungs moves the muscles which are attached to the ribs, and in some cases in this way greatly modifies the form of the bones.

Another example of a mechanical influence is seen in the blood. The weight of blood in the body is not great; but it is the amount of nutriment sufficient to maintain healthy dialysis in all the tissues. The whole of the blood makes its way into the lungs, where it apparently loses bulk and gains temperature. Under the heated condition it is driven through the body in the arterial vessels by the left ventricle, and therefore exercises an intermittent (pulsating) pressure not only upon the arteries themselves, but, in a quieter way, upon the tissues adjacent to them. That this muscular power has a mechanical effect upon growth is shown in the heart itself, by growth being continuous throughout life. The return of the blood to the heart is facilitated by its decreased temperature lessening its bulk, by the material left in the tissues, as well as by the pump-action which passes it into the lungs and enables the lymphatics to pour in new material. Evidence of its mechanical power in producing growth is well seen in the thickening of arterial walls in the condition named aneurism.

These are some of the chief mechanical engines of the body which are capable of influencing the skeleton. That they actually produce by their mechanical action the phenomena of growth which theoretically they are sufficient to produce is not capable of elaborate proof in the healthy individual, because, from the deep-seated position of the changes, they cannot usually be observed. Yet, in the case of athletes and gymnasts, it is observed that, with exercise, the whole body becomes heavier, and the circumference of the chest permanently greater; and often special muscles are seen in a short time to augment visibly. This may be observed in the legs of women who dance and the thighs of men who ride. But to see the effect upon the bones, it is necessary to contrast the skeleton of the wild animal, where the muscles are used with great power, with the skeleton of the tame animal, where the muscles have more limited action; and then it will be seen that powerful crests and processes on the bones are developed in direct proportion to muscular activity. Moreover Professor Humphry finds that bones are densest in those parts which are subject to the greatest mechanical stress, and hardest in those persons who are strongest and most active—and that the bones are most curved in those persons whose muscular strength is greatest, while weak persons, on the contrary, have comparatively straight bones. But, important as this kind of evidence is, it gives but a poor idea of the potency of this power to produce growth when circumstances are specially favourable.

In the case of muscles, the most wonderful example is afforded by the increase of the uterus in the exercise of its function, and its rapid degeneration when that function is completed.

In the case of bones, an example no less wonderful as an increase, but not so obviously due to a local function as to an hereditary condition of the body, is afforded by the antlers of the male deer; and no more striking example could be afforded of the dependence of growth upon nutrition, which under other circumstances these mechanical actions increase, than is seen in Hunter's experiment, the transplantation of the spur of the cock to its comb, where the spur grows vigorously, and in one case has attained, in a spiral form, a length of 6 inches.

These and such like considerations have not escaped the attention of some of the greatest physiologists and best observers of the body in health and disease, and have led them to advance, on inductive evidence, views of growth identical with those which are here urged deductively. Thus Sir James Paget finds that growth is due to intermittent pressure, which approximates the state of the tissue towards that of inflammation, but does not actually in healthy growth reach the inflammatory state.

In the last instances adduced, examples have been given of the result of altered nutrition upon growth, where that alteration was not due to mechanical action. Now we may notice some individual cases in which the dialyzing action called nutrition becomes altered abnormally, and parts change their characters so as to present in the individuals of a species processes similar to those which are normal in comparative anatomy. In some of its aspects pathology might be called an inverted palæontology.

Thus Sir J. Paget concludes that "when any of the long bones of a person who has not yet attained full stature is the seat of disease attended with unnatural flow of blood in or near it, it may become longer than the other or more healthy bone." And in one case where one segment of a leg was defective in growth, another segment lengthened to supply the deficiency. But the examples of hypertrophy of bones from disease are not numerous; and in rickets only an inflammatory thickening of the bones takes place. Still the cases are many in which increased osseous growth takes place in consequence of the inflammatory condition induced by fractures.

Mr. Hawkins refers to some curious cases in which muscle becomes changed into bone by a simple inflammatory action. Thus a surgeon in the Prussian army found that in 18 out of 600 recruits there was a swelling of the deltoid and pectoral muscles in front of the shoulder, due to the pressure and irritation induced by first carrying the musket, and that in these cases pieces of bone were deposited, from 2½ to 7 inches long, which were removed by operation. He mentions the case of a boy in whom the least blow would cause an exostosis or ossification of a muscle or ligament; and, finally, details a case where his patient, after getting wet, became liable to painful swellings which eventually became the seats of ossification. One such bone, between the rhomboid and trapezius, and extending from the scapula to about the sixth vertebra, was removed: it had the microscopic and chemical characteristics of true bone, consisted to a small extent of cartilage, had the usual dense outer shell, which was covered with periosteum, into which the muscular fibres were inserted, as in natural bone. And Sir J. Paget refers to a specimen in the College of Surgeons in which nearly all the muscles of the back were ossified. He supposes that the osseous deposit originally took place in the connective tissue, and by its growth through pressure produced atrophy and destruction of the proper muscular substance. Ossification of the ligaments is very common among all animals; and Mr. Hawkins refers to numerous ossific deposits in the cellular tissue behind the pleura, and to a case in which the lungs have great masses of bone in them, occupying at least a third of their bulk. And a case was recorded by Dr. Allbut in which the lung was full of well-developed bones.

The other normal tissue which is commonly produced in the body by disease is fat. This, to a considerable extent, may replace all the muscles and all the bones. In one case, all that remained of the upper part of a femur, after boiling, is described as scarce any thing besides a great quantity of white crystalline fatty matter. Occasionally the bones lose their osseous matter without any fatty substitution.

These pathological illustrations of variety in growth have their chief interest in the proved hereditary character of disease (often symmetrical). In the case of fatty degeneration, from that condition supervening as a consequence of inactivity, it is suggestive, as showing the way in which structures which are no longer or less used may be got out of the body, perhaps not in one but in successive generations. Even the heart reduces its size in accord with the amount of blood which it has to circulate. The bones in the individual, according to Prof. Humphry, most effectively reduce their length by such disease as obliterates the epiphysial lines, while their thickness decreases by cessation of muscular action.

Growth also has a local morphological aspect. Thus Edentates, Cetaceans, Chelonians have the bones of the skeleton solid; most mammals and most living reptiles have medullary cavities in their long bones, while in most birds these cavities become chambers into which prolongations of the membrane covering the lung extend. It is necessary to remark that Edentates and Chelonians are comparatively inactive animals, and that Cetaceans move in a comparatively unresisting medium, so that, however active, their muscular labour is light; and that birds, as a rule, are far more active than mammals. Now in mechanics there is a law (clearly stated as a mechanical law by Mr. Herbert Spencer), the law of the neutral axis, by which, if a substance is exposed alternately to pressure in opposite directions, there will be at the outsides alternate pressure and tension, and in an internal part (of varying extent according to the substance strained) the neutral axis which experiences compressions only.

Now we have seen that the alternation of pressure and tension is the condition of growth, and compression the condition of atrophy. Hence it may be inferred that the solidity of bones will be in the inverse proportion to the activity of the muscles which are attached to them; or, speaking generally, the hollowness of bones is in direct proportion to the activity of the animal, the compressions at the neutral axis necessarily resulting in atrophy of the bone there. Among flexible trees, the law of the neutral axis is seen in the formation of pith.

Another special condition of bones, is that in some animals they become composite—that is, develope special and terminal parts or plates called epiphyses, which sometimes subsist throughout life, and are sometimes obliterated as the energy of growth declines. Thus, in the internal skeleton of *living* Chelonians and Crocodiles I have not noticed any appearance of separate terminal ends; while if certain bones of crocodiles are compared with others of some marsupial mammals, there will be seen, with a close resemblance of form, separate bone-elements in the mammal, which make the articular ends. Such separate elements may be seen in amphibians, lizards, many mammals, and, rarely, perhaps, in some birds. Why this difference? Of course we naturally infer that the kind of pressure and tension which ossified the bone originally sets up in the articular cartilage (or elsewhere) the same kind of action within its substance by the mechanical power of locomotion. Dr. Humphry states that epiphyses appear at the sternal ends of the clavicles; but they are not there in childhood while growth is going on in a normal way, but are only developed when the chest is undergoing its greatest lateral expansion, in the years from 17 to 20, when they become anchylosed to the shaft of the bone. And in many heavy-bodied active animals, like the buffalo, rhinoceros, &c., the rib terminates at its head in an epiphysis, which articulates with another epiphysis on the neural arch; while in light-bodied animals no such epiphyses are met with. And wherever epiphyses are found, whether as terminal of bones or as places for the attachment of powerful muscles, it is only where pressure and tension are manifested under conditions of great activity of the part. This new bony growth takes place towards the articular termination of the cartilage, where the subinflammatory condition is induced by local activity—and so, while giving a means for the articular ends of bones to become better adapted to each other, protects the epiphysial cartilage and furnishes it with an additional surface on which bony growth may take place. From which considerations it would appear that one ossification may develope another upon itself whenever the forces manifested at its ends (or elsewhere) are more than sufficient to continue simple growth by increase on the normal surface. Small ossifications are often met with about the joints in many parts of the body, which have originated in this way. The fact of epiphyses being only characteristic of certain species of animals in each class shows us that they have no necessary connexion with the animal grade of organization; the fact of their appearing under conditions of unusual activity shows that their origin is the same as that of all other bones, but that they are of subordinate importance in the skeleton, since they become united to the normal skeletal elements, and do not necessarily modify the form of their terminal ends.

I now notice the general morphology of bones and its relation to mechanical causation.

Mr. Charles Darwin finds that the domestic races of pigeons, fowls, and ducks, which fly little, have the chief bones to which are attached the muscles which are exercised in that function smaller and lighter than in the parent races. Similarly it is observed that, in the improved races of pigs, shortened legs and snout, and altered form of the occipital condyle, may be attributed to the parts not having been fully exercised; for the highly cultivated races do not travel in search of food nor root up the ground with their ringed muzzles. Also domestic rabbits have the body and whole skeleton larger and heavier than the wild animal, and the leg-bones are heavier in proportion; but neither the leg-bones nor scapulæ have increased in length proportionally with the increased dimensions of the remainder of the skeleton. All of which is in accord with the law of pressure and tension, the increase of bulk of the tame animal depending merely on luxuriant diet. The leg-bones, less exercised, experience less central compression, and are consequently relatively heavier; and similarly, from less exercise of the parts usually most exercised, they become relatively shorter. And with respect to cattle, Prof. Tanner finds that in improved breeds the lungs and liver are considerably reduced in size when compared with those organs in animals having perfect liberty—thus changing the form of their bones by respiration and nutriment.

But the kind of evidence which more particularly concerns the subject now is the converse of this. Thus ungulate animals which are light of body (deer, horses, &c.) have the limbs longer than have most unguiculate animals; and as a rule, those hoofed animals are more active, and strike the ground with greater force, so that the bones can act on each other more powerfully. And in man, where the position of the body is erect, and the habit not active, so that the weights of the upper parts of the body act on each other with no violent pressure, and that alternating with rest in sleep, the vertebræ will be seen to steadily enlarge, from the neck down to the sacrum. But in quadruped animals with a large head carried erect in running and pendent in seeking food, like the deer, the cervical vertebræ will be seen to be longer and larger than the dorsal vertebræ; and here it is to be remarked that the neck-bones have to support the weight of the head, and that their processes experience the pressure and tension caused by its movements, while the back-bones only have to share between them the general weight and tension of the carcass. In animals which walk erect, and chiefly use the hind limbs, the hind limbs are longer than the fore limbs, as in man and the ostrich, and in jumping animals, such as kangaroos, jerboas, frogs, &c. On the other hand, animals which use their fore limbs more than the hind limbs, have them longer than the hind limbs: familiar examples of this condition are seen in the tribe of bats and in most birds, such as the albatross or the swan. Here the pressure and tension experienced by the bones in flight is very great in comparison with the influences which could stimulate growth in the hind limbs; and the growth is greater.

Special modification of structures in relation to modified function may be seen in the humerus of the burrowing mole: this bone experiences enormous lateral tension, and accordingly attains enormous width from side to side. The animal's method of burrowing causes a great use of the pectoral muscles; and the use of these muscles coincides with the condition of their attachment for the development of a sternum similar in form to that of a bird; and true coracoid bones are attached to it, as in birds. In quadruped animals which carry the head and neck erect, like the giraffe, where the vertebræ experience the weight of the head and part of the neck above each in pressure, made intermittent by activity, the vertebræ are found to attain enormous length; but the upper bones are the longer ones: whence it may be inferred that a moderate intermittent pressure is more favourable to growth than a considerable pressure, the greater pressure producing what is relatively atrophy; and in the elephant, where the pressure of the head upon the vertebræ is great, and not greatly varied, the force of growth is unable to overcome the weight, and the vertebræ are short from back to front, though they grow at their circumference. The same shortening of the neck-vertebræ, connected with the continuous pressure of a large head, is admirably seen in the Cetacea, where in progression the neck-vertebræ have to support the non-intermittent pressure of the immense head. Whatever and wherever the pressure and tension are manifested, it is always with this result in increase or decrease of growth, which vary as the pressure is intermittent or constant. Examples of it could only cease when the enumeration of organisms was terminated.

But the inference from these facts is not merely that the same law holds true for growth in the different parts of the skeleton and in the whole skeleton as governs the growth of a single bone and of its parts, but that the whole distinctive plan of the part which is inherited from individual to individual is as completely in harmony with this law of growth as though it had been produced not by inheritance at all, but wholly by mechanical causation, in the individual animal in which it is visible; that is, growth in the individual and growth in the plan of the individual are commonly in the same directions, and such as would have been produced by the continuous action of the same cause, namely intermittent pressure and tension. But it is seen that only an infinitesimal element of the plan of the animal *is* produced by the individual; hence, since the plan-growth exists in all the individuals of a group, it is justly inferred that the plan has accumulated in the sum of the individuals by being passed on from generation to generation; for in that way, and in that way only, could the mechanical law act which has been seen to have acted in the daily life of animals, so as to produce the forms of special parts in accord with the conditions of mechanical causation which we found to characterize regions of the body.

Finally, it will conduce to clearness to show the kind of way in which structures are inherited, so as to get the results of persistent modifying causation accumulated. The individuals of that common bond called a species, though nearly resembling each other, as is well known, have differences so marked that it is rare for the eye to be unable to distinguish them; so that the variation of a species is enormous: and if this variation, instead of being in a multitude of different directions, be in any manner caused to be chiefly of the same kind, obviously the mere summing of the variation will produce most extensive differences. Here it is necessary to remark that in every family there may be seen two kinds of variation among the children,—first, that which depends upon the individual peculiarities of nutrition, and which gives a different aspect to brothers and sisters, and then that kind of inheritance by which the child reproduces the mental and physical form and distinctive peculiarities of the parents. And when the variation in nutrition coincides with the distinctive peculiarities in inheritance, these latter will be specially intensified. And it is found by experiment that the accumulation of characters by inheritance has an influence in fœtal development by which parts may be multiplied. It is probable that the epiphyses of bones thus take their origin; and it is certain that increase in the number of vertebræ is thus instituted. Upon this point Mr. Charles Darwin's observations upon pigeons are specially instructive. Pigeon-fanciers have gone on selecting *pouters* for the length of their bodies; and it is found that their vertebræ are generally increased in number, and their ribs in breadth. The *tumblers* have been selected for their small bodies; and their ribs are generally lessened in number. *Fantails* have been selected for their large, widely expanded tails with numerous tail-feathers; and the caudal vertebræ are increased in size and number. From which it seems to me evident that the special exercise of a function in life sometimes produces an increase of structure in reproduction, beyond that which was possible to the parent from the plan of its structures.

The variation from nutrition in reproduction sometimes goes so far that a tissue is dialyzed with its characters so far intensified as to be both unlike the parent and all others of its species. Two cases quoted by Mr. Darwin illustrate this. First, there is Lambert, the porcupine-man, whose skin was covered with warty projections which periodically moulted, and whose six children and two grandchildren were similarly affected; and there is the Burmese family observed by successive ambassadors at the court of Ava, where father, daughter, and grandson had the body, with the exception of the feet and hands, covered with long, straight, silky hair. And from these and many similar cases it would seem a natural inference that, just as the bones and dermal covering vary with altered nutrition, so also do all other parts of the organism, which are less easily observed.

In conclusion, it has been seen that growth depends upon a kind of organic dialysis, called nutrition, which is sustained throughout the body by the mechanical actions of the parts of the organism which produce pressure and tension, while the direction in which this action is manifest is due to the common plan on which the individual is built. And the amount of the change is due to the change of structure produced in the individual by changed function inherited in the offspring, and partly by the realization in the offspring of such structures as the parent's functions tended to produce, but which its common plan rendered impossible for itself to develope. And with this condition of variation, the general inference from the phenomena of growth is, that the form of the whole skeleton, as of every bone, is due to the mechanical strains to which it is subjected, since these govern its nutrition.

[To be continued.]

---

## XXIX.—*On the Nomenclature of the Foraminifera.* By W. K. Parker, F.R.S., and Prof. T. Rupert Jones, F.G.S.

[Continued from p. 230.]

*Nummulitic Limestone of Gyzeh and Mokattam**. (Abhandl. Berl. Akad. Wiss. 1838, p. 93, tables XIV. XVI. pl. 4. fig. vii.)

Pl. xxiii. fig. 1, *Miliola sphæroidea* ("compare *Cenchridium oliva*, 1843"), and fig. 2, *M. ovum*, are both *Lagena globosa*; but the second specimen is longer in proportion (oval-oblong). Fig. 3, *Textilaria globulosa* (1838), *α*, fig. 4, *β. obtusa*, fig. 5, *γ. amplior*, fig. 6, *δ. dilatata*, are *Text. globulosa*, Ehr. Fig. 7, *T. linearis* ("*T. striata*, 1838, is known only in fragments"), fig. 8, *Grammostomum polytheca* (?), figs. 9 & 10, *Gr. ægyptiacum*, figs. 11 & 12, *Gr. angulatum*, fig. 13, *Gr. falx*, fig. 14, *Gr. siculum* (?), fig. 15, *Gr. increscens*, fig. 16, *a*, *b*, *Gr. poly-*

* See Mr. Bauerman's section of the Mokattam Cliff, Quart. Journ. Geol. Soc. London, vol. xxv. p. 40, where references are made to the works of Figari Bey and Oscar Fraas. See also Russegger's 'Reisen in Europa, Asien, und Afrika,' &c. 5 vols. and Atlas, 1841–42.